

## Bilateral gynandromorphs, sexual and/or color mosaics in the tiger swallowtail butterfly, *Papilio glaucus* (Lepidoptera: Papilionidae)

J. Mark Scriber<sup>1</sup>

and

Mark H. Evans

Department of Entomology, University of Wisconsin, Madison, WI 53706

<sup>1</sup>Current address and reprint requests to:

Department of Entomology, Michigan State University, East Lansing, MI 48824

### Introduction

Mosaic specimens of Lepidoptera may be of a sexual nature (gynandromorphs or intersexes) or homeotic (involving an inappropriate location for a particular feature or pattern; see reviews by Sibatani, 1980, 1983a, b). Intersexuality typically arises from development errors late in development, and involves an individual which possesses a mosaic of traits, some of which are female, and some of which are male (see McCafferty and Bloodgood, 1986). Gynandromorphs generally develop a sex abnormality much earlier in development; when this occurs at the formation of one of the first two blastomeres, it is possible for individuals to become bilaterally differentiated with one half male and the other half female (Clarke and Ford, 1980; Ayala and Kiger, 1984). The relationship between intersexual mosaics and gynandromorphs is not entirely clear, partly because of the infrequent occurrence of both (Ford, 1955). The combined use of laboratory crosses of species or subspecies, and the recent development of a technique to monitor the heteropyknotic 'Smith' (S) body in the nucleus of somatic cells (derived from the Y-chromosome of female Lepidoptera) should contribute to our understanding of the development of these abnormalities (see Cross and Gill, 1979; Clarke and Ford, 1980, 1983; Bull, 1983).

From the Papilionidae (see Table 1) gynandromorphs have been reported from *Papilio polyxenes asterias* Stoll (Edwards, 1984; Blau, 1978; and Wm. Bergman, pers. comm.); *Ornithoptera victoriae* Gray, and *O. priamus* L., (Schmid, 1973), *O. croesus* Wallace (Parrott and Schmid 1984), *O. poseidon* (D'Abrera 1976); *Parnassius autocrator* (Sbordoni and Forestiero, 1984); *Papilio androgeus* (Sbordoni and Forestiero, 1984) and *Papilio glaucus* L. (Skinner, 1919; Cockayne, 1935; and Clarke and Clarke, 1983). In addition to these published records of gynandromorphs and a large number of additional records reviewed by Cockayne (1935), several hundred sexually mosaic and bilateral gynandromorphic specimens exist in the Lepidoptera collection of James R. Neidhoefer (housed at the Milwaukee Public Museum).

Table 1. Gynandromorphs (Lepidoptera) reported in the literature.

Family	Genus species	References
Saturniidae	<i>Automeris io</i> Fabricius <i>Eacles imperialis</i> Drury <i>Callosamia promethea</i> (Drury)	Cassino and Reiff, 1917, Hessel, 1964; Muller, 1966; Manley, 1977
Pyralidae	<i>Hedylepta accepta</i> (Butter)	Riotte, 1978
Geometridae	<i>Phaeoura mexicanaria</i> (Grote) <i>Antepione thisoaria</i> (Guenee)	Blanchard, 1969; Durden, 1984
Lymantriidae	<i>Lymantria dispar</i> (L.)	Muller, 1976
Nymphalidae	<i>Limenitis weidemeyerii latifascia</i> L. <i>L. arthemis-lorquini</i> (Boisduval) <i>L. arthemis-astyanax</i> (Fabricius) <i>Speyeria atlantis dodgei</i> (Gunder)	Grey, 1959; Perkins and Perkins, 1972; Platt, 1983; H. Romack pers. comm., 1984
Pieridae	<i>Conopteryx rhamni</i> L. <i>G. cleopatra</i> . L. <i>Pieris brassicae</i> L. <i>P. protodice</i> Bdv. & LeC <i>P. rapae</i> L. <i>Colias christina</i> Edwards <i>C. eurytheme</i> Bdv. <i>C. philodice</i> Godart <i>Pontia daptidice</i> (L.) <i>Tatochila steradice</i> Stgr.	Emmel, 1964; Hovanitz, 1965; Nekrutenko, 1965; Shapiro, 1970; Gardner, 1972; Sbordonni and Forestiero, 1984; Shapiro, 1978, 1981, and 1985.
Hesperiidae	<i>Polistes mystic</i> (Scudder) <i>P. origines</i> (Fabr.) <i>Erynnis horatius</i> Scudder & Burgess <i>Hesperia columbia</i> (Scudder)	Nielsen, 1977; Israel and Cilek, 1982; Scott, 1986
Lycaenidae	<i>Strymon bazochii</i> Godart <i>Lycaena gorgon</i> (Boisduval) <i>Agriades rustica rustica</i> (Edwards) <i>Mitoura gryneus</i> (Hubner) <i>Celastrina ebenina</i> Clench <i>Cyaniris semiargus</i> (Rott.) <i>C. argiolus</i> (L.)	Opler, 1966; Riotte, 1978; Rahn, 1982; Sbordonni and Forestiero, 1984; Shuey, 1984; Shuey and Peacock, 1985
Papilionidae	<i>Papilio polyxenes asterias</i> Stoll <i>P. glaucus</i> L. <i>P. androgeus</i> Cramer <i>Ornithoptera victoriae</i> <i>O. croesus</i> Wallace <i>O. poseidon</i> Doubleday <i>O. priamus</i> L. <i>Parnassius autocrator</i> Avinoff	Skinner, 1919; Schmid, 1973; Cockayne, 1935; Blau, 1978; W. Bergman, pers. comm. 1983; Clarke and Clarke, 1983; Sbordni and Forestiero, 1984; Parrott and Schmid, 1984; D'Abbrera, 1976

Table 2. Progeny (1982 reared) of pairing #9 (*P. g. glaucus* yellow morph female x *P. g. canadensis* male; see text for further details).

Ecllosion year	Bilateral		Males		Females		Dead pupae	Pupae still alive
	Gynandromorph		eclosed	pharate <sup>1</sup>	eclosed	pharate <sup>1</sup>		
1982	0		7	0	0	0	4	0
1983	1		2*	4	6	1	8	0
1984	0		0	0	6	0	0	0
(Total)	(1)		(9)	(4)	(12)	(1)	(12)	(0)

\*One of these males had asymmetrical external valvae.

<sup>1</sup>pharate = adults dying inside the pupal case with wings formed.

Table 3. Progeny (1983 reared) of pairing #628 (*P. g. glaucus* dark morph female x *P. g. canadensis* male; see text for further details).

Ecllosion year	Bilateral Gynandromorph	Males		Females		Dead pupae	Pupae still alive
		eclosed	pharate <sup>1</sup>	eclosed	pharate <sup>1</sup>		
1983	0	13	0	0	0	9	-
1984	1	25	0	4	0	10	-
1985	0	0	0	13*	0	3	-
(Totals)	(1)	(38)	(0)	(17)	(0)	(22)	(20)

\*One of these females is a "yellow intermediate" and one is a "dark intermediate", between the two typical color morphs while all other females are typical yellow morphs (see also Scriber et al, 1987).

The bilateral gynandromorphs in this collection alone include 49 Pieridae, 70 Nymphalidae, 6 Hesperidae, 20 Lycaenidae, 1 Danaidae, and 11 Papilionidae (S. Borkin and A. Young, pers. comm.).

It has been suggested that either viral diseases (Gardiner, 1972; Blau, 1978; Sevastopulo, 1973) or parasitism, and/or abnormal temperatures could be responsible for inducing such abnormalities (Riotte, 1978). It has also been observed that bilateral gynandromorphs and mosaics can occur in multiples from the same brood (Cockayne, 1935; Ford, 1955; Sevastopulo, 1973) and that a variety of laboratory hybrid crosses have yielded intersexual or gynandromorphic individuals (Standfuss, 1900; Whicher, 1915; Cockayne, 1935; Clarke and Sheppard, 1953, 1960; Clarke et al., 1977; Clarke and Ford, 1980; Platt, 1983).

Sir Cyril Clarke and colleagues have been investigating the genetic basis of abnormal wing coloration in *Papilio glaucus* for decades (see Clarke and Clarke, 1983 for a review), and they point out that color mosaics and gynandromorphs are sometimes strikingly visible in *P. glaucus* because of the marked differences between the yellow background of males and yellow morph females and the black/brown background of dark morph females. The Herman Strecker collection (currently on loan from the Chicago Field Museum to the Allyn Museum in Florida) contains a number of such mosaics. This valuable collection, which was assembled during the second half of the 19th century, contains a number of *P. glaucus* mosaics previously described and/or reported upon the literature (e.g. Strecker, 1878; Ehrmann, 1894; Walsten, 1977; Ehle, 1981; Shapiro, 1981b). Edwards (1884) also figures an individual with  $\frac{1}{2}$  black and  $\frac{1}{2}$  yellow which he describes as a female (Edwards, 1868). Clarke and Clarke (1983) figure similar specimens (essentially half yellow/half dark) from the Strecker collection, one of which is a color mosaic female (from Indiana) and the other an apparent gynandromorph from Pennsylvania.

Partial color (sex?) mosaics in *Papilio glaucus* are also rare, but have been collected in Pennsylvania and previously described by Strecker (1878), and figured by Walsten (1977), Ehle (1981), and Clarke and Clarke (1983). In addition to the partial color mosaics we report here (see also Scriber et al, 1987a), additional cases for *Papilio glaucus* are

known to exist (e.g. personal collections of James Sternberg and David Ritland). The Milwaukee Public Museum contains two partial mosaics of *Papilio glaucus* reared by E. Dluhy in Chicago, Illinois. It is intriguing that the few cases of female coloration patterns unlike their mother's which Clarke and Sheppard (1962; see also Clarke et al., 1976) encountered in their studies were all tracable to a group of pupae obtained from E. Dluhy (from Chicago, Illinois). It was suggested (Scriber et al, 1987a) that similar chromosomally abnormal stock might be involved in both the color mosaics and the abnormal segregation of dark and/or yellow female forms of *Papilio glaucus*. We now feel that an explanation for this abnormality may involve introgression between *P. g. canadensis* and *P. g. glaucus* subspecies near the "blend zone" in Wisconsin (Scriber 1982, 1983) and across the Great Lakes region (Scriber et al., 1987b). In this paper we shall report aspects of our laboratory studies with members of the North American tiger swallowtail, *Papilio glaucus* L., group.

## Methods

In the past 6 years we have reared through to the adult stage or collected in the field (from southern Florida to northern Canada) over 28,000 specimens of the *Papilio glaucus* species complex. Field captured specimens have included all three *P. glaucus* subspecies as well as *P. eurymedon*, *P. rutulus*, *P. multicaudatus*, and *P. alexiars garcia*. Lab reared specimens have included pure stock of all of these species and subspecies as well as geographic site crosses within subspecies, subspecies-level and species-level crosses.

Oviposition by adult females is induced by placing each wild-captured or hand-paired female into its own clear plastic box (approximately 10 cm deep × 15 cm × 30 cm) with a moist paper towel and selected larval foodplant leaves. Leaf turgor was maintained in these plants by use of floral aquapics® (water-filled plastic vials with a rubber cap, through which leaf petioles or small branches can be inserted; see Scriber, 1977). Heat and light were provided by incandescent bulbs placed at a distance of approximately 0.3-0.5 meter from the plastic boxes.

Larvae were reared to pupation on one of various foodplants, (leaves were changed three times per week) under controlled environment conditions (16:8 photo-scoto-phase with corresponding temperatures of 23°/19°C, respectively). Pupae were weighed 2 days after pupation (the weight subsequently serving an identification number for the individual) and then placed in individual cylindrical screen cages (15 cm diameter × 12 cm height) under larval rearing conditions or similar laboratory conditions (21-24°C) to permit development and eclosion as adults. Direct developing individuals normally emerged within 2-3 weeks after pupation. Other pupae were given at least 6 weeks before being refrigerated in darkness (at 40-45°F for 3 months or more) to break diapause. Hand-pairings were generally attempted 12-48 hrs after adult female eclosion and 2-3 days after male eclosion. Since dark female color suppression and obligate diapause are linked on the X-chromosome (R. Hagen and J.M. Scriber, manuscript), we observe one year delayed emergence of F<sub>1</sub> females from both yellow (Table 1) and dark (Table 2) females when mated with *P.g. canadensis* males.

Table 4. Gynandromorphs, mosaics, and their siblings (1981-1986).<sup>a,m</sup>

Brood #	Rearing Year	Siblings in the Brood							
		Gynand.	Mosaics	Fig. #	Males	Yel	Dk	Pupae (as of 7 Nov. 86)	Dead Pupae
9	82	1		1	13 <sup>b</sup>	13	0	0	12
628	83	1		2	38	17 <sup>c</sup>	0	20 <sup>d</sup>	22
631	83	1		10	6	6	0	2	3
1091	84	1		4	2	0	1	0	0
2025	84	1		9	1	2	0	0	0
2830	85	1		7	40	0	0	22	3
3622 <sup>e</sup>	86	1		6	8	0	18	9	0
3935	86	1		8	6	0	11	13	0
4196 <sup>e</sup>	86	1		5	26	1	10	20	0
4210	86	1		3	31	2	27	4	3
JMS	81		1	11	5	0	12 <sup>n</sup>	0	0
658	83		1	14	7	0	10	1	0
688	83		14	20	22 <sup>f</sup>	0	24 <sup>g</sup>	34 <sup>h</sup>	6
717	83		1	29	30	0	34	0	1
1064	84		1	12	9	0	11	0	1
1128	84		1	15	16	0	24 <sup>i</sup>	0	1
1348	84		1	28	22	18 <sup>j</sup>	0	2	0
1351	84		1	27	52	37 <sup>j,k</sup>	1	24	7
1534	84		1	26	0	0	0	0	0
1905	84		1	X	23	0	31	3	7
1914	84		1	23	42	0	41	14	2
1999	84		1	13	9	0	6	0	1
2030	84		1	X	7	0	2	0	0
3122	85		1	X	1	0	0	0	0
3604	86		1	24	11	0	15	18	0
3770	86		1	25	34	0	3 <sup>l</sup>	28	0
3800	86		1	17	29	0	28	19	1
3973	86		1	16	19	0	15	6	0
4230	86		1	30	8	2	8	1	0
Subtotals:		10	32		512	98	320	240	70
Total Reared to pupae = 1282									

<sup>a</sup>Pharate adults are included with "emerged adults".<sup>b</sup>One male has asymmetrical valvae.<sup>c</sup>One female is a "yellow intermediate" and one is a "dark intermediate".<sup>d</sup>Two of these pupae are unaccounted for as of 1984.<sup>e</sup>An additional emerged adult has no sex recorded on printout.<sup>f</sup>One male has very reduced claspers and one male has extra dark scaling.<sup>g</sup>Two females are slight intermediates and one female has extra yellow and unusually high density blue.<sup>h</sup>Approximately 6 weeks after pupation, these were refrigerated to break diapause and not brought out of the refrigerator the first time until 14 mos. later. Although they still appear viable, it is uncertain if they will close in the future.<sup>i</sup>One female is a dark intermediate.<sup>j</sup>Some of these may be "yellow intermediates" but did not get recorded as such. They are not all pinned now and colors cannot be easily verified.<sup>k</sup>Four females are "yellow intermediates" (i.e., more yellow than dark).<sup>l</sup>Two females are "dark intermediates" (i.e., more dark than yellow).<sup>m</sup>Wild collected mosaics (see Table 3) are excluded from this table as they have no sibling data.<sup>n</sup>Two females were "dark intermediates".

Table 5. Phenotype, geographic origin, and brood number of gynandromorphs.

Phenotypes &/or geographic origins <sup>a</sup>	Gynandromorphs		Brood # b generating aberrant
	Perfect Bilateral	< 50% one sex	
Georgia		1	2025
Ohio		3	631 3622 3935
Texas		1	1091
Pa Yel x Pgc (Juneau)	1		9
S. Car Dk x Pgc (Marinette)	1		628
Ill. Dk x F <sub>1</sub> (GaDk x Pgc)		1	4196
W. Va. Dk x <i>P. rutulus</i>		1	2830
Ohio Dk x <i>P. alexiaries</i>	1		4210
Totals	3	7	

<sup>a</sup>When phenotype or geographic site crosses are listed, the female background is listed first.

<sup>b</sup>For information on siblings of aberrants, look up brood numbers on table #1.

## Results

Of the 28,000 reared adults we have observed 10 gynandromorphs and 32 color mosaics (Tables 4 and 5). Of the obvious gynandromorphs four of the five perfect or near perfect bilateral gynandromorphs (Figs. 1-5) were progeny of subspecies of species crosses. The fifth could also be considered a subspecies cross if the Texas population is *P. g. australis* (Scriber, 1986). Of the remaining five gynandromorphs (Figs. 6-10) only one (Fig. 7) involves two different taxa. Of approximately 8,500 field collected specimens during 1981-1986, we have never collected an obvious gynandromorph.

Of the 32 color mosaics listed in Table 4, all but 6 are of either pure *P. glaucus glaucus* or *P. g. australis* (Table 6). These mosaics are dark morph females with varying amounts of yellow dorsally and/or ventrally on their wings or body. Of the 37 total *P. glaucus* mosaics, one was a field collected *P. g. australis* from Highland Co., Florida (Fig. 22) and two were field collected *P. g. glaucus* from Dane Co., Wisconsin (Figs. 18

Table 6. Phenotype, geographic origin, and brood number of color mosaics.

Phenotypes &/or geographic origins <sup>a</sup>	Gynandromorphs		Brood # b generating aberrant
	Dk exceptional color	w/ yellow	
Georgia	3		1064 2030 3122
Illinois	2		1905 1999
Ohio	4		658 1128 3800 3973
Texas	2		1039 (wild) 3270 (wild)
Wisconsin	17 <sup>c</sup>		JMS 688 729 (wild) 736 (wild)
Georgia x Ohio	1		3604
(Ga. x Wis.) x Ill.	1		1914
<i>P. glaucus australis</i>	1		no # (wild)
Ga. Dk x Pgc (Green Lake)			1348
Ga. DK x Pgc (Tompkins)	1 <sup>e</sup>		3770
Tx Dk x Pgc (Juneau)		1	1534
Tx Dk x Pgc (Wood)		1	1351
B <sub>1</sub> (F <sub>1</sub> (GaDk x Pgc) x Wis.) x Pga	1		717
Ill Dk x <i>P. alexiaries</i>	1		4230
Totals	34 <sup>f</sup>	3	

<sup>a</sup>When phenotype or geographic site crosses are listed, the female background is listed first.

<sup>b</sup>For information on siblings of aberrants, look up brood numbers on table #1.

<sup>c</sup>Of these 17 mosaics, 14 were siblings in brood #688.

<sup>d</sup>Counties of specimen origin are shown in parentheses and all are Wisconsin except Tompkins which is New York.

<sup>e</sup>This is actually an intermediately colored specimen but the exceptional color is yellow.

<sup>f</sup>Of the 34 dominantly dark color mosaics listed, 27 are shown in the following illustrations. (All other aberrants in this table are illustrated).







Fig. 1. A bilateral gynandromorph (from brood #9, pupal wt. 1.0605, ex ova, reared in 1982, eclosed on 21 May 1983) from a lab cross of a yellow morph *P. g. glaucus* female (2nd generation lab-reared from wild stock collected by W. Houtz in Schuylkill Co., Pennsylvania) mated to a wild collected male *P. g. canadensis* from Juneau Co. Wisconsin. A) dorsal, B) ventral.

Fig. 2. A bilateral gynandromorph (from brood #628, pupal wt. 0.9310, ex. ova, reared in 1983, eclosed on 30 May 1984) from a lab cross of a dark morph *P. g. glaucus* female (reared from eggs obtained from a wild dark morph female collected by R. Peigler in Pickens Co., South Carolina) mated to wild collected male *P. g. canadensis* from Marinette Co., Wisconsin (collected 1-5 July 1983 by Don Caine). A) dorsal, B) ventral.

Fig. 3. A bilateral gynandromorph (from brood #4210, pupal wt. 1.1099, ex. ova reared in 1986, eclosed on 26 Sept. 1986) from a lab cross of a dark morph *P. g. glaucus* female (2nd generation lab reared from wild stock collected by J. Thorne and MHE in July 1985 in Adams Co., Ohio) mated to a wild collected male *P. alexiaries garcia* from Nuevo Leon, Mexico (collected 2, 3 Aug. 1986 by W. Warfield, D. Robacker and MHE). A) dorsal, B) ventral.

Fig. 4. A nearly perfect bilateral gynandromorph, or sexual mosaic, (from brood #1091, pupal wt. 1.1493, ex. ova, reared in 1984, eclosed on 27 June 1984) from a wild collected dark morph *P. g. glaucus* female from Jasper Co., Texas (collected on 9 April 1984 by JMS and MHE). A) dorsal, B) ventral.

Fig. 5. A gynandromorph, or sexual mosaic, which appears to be more than 50% female (from brood #4196, pupal wt. 1.2779, ex. ova, reared in 1986, eclosed on 29 Sept. 1986) from a lab cross of a dark morph *P. g. glaucus* female (reared from eggs obtained from a wild dark morph female collected by M. Berenbaum in Champaign Co., Illinois in June 1986) mated to a subspecies hybrid male (whose mother was the daughter of a dark morph *P. g. glaucus* female collected in Georgia in Aug. 1985 by J. Maudsley and whose father was a *P. g. canadensis* collected in Lincoln Co., Wisconsin on 3 June 1986 by D. Ware, V. Viegut and MHE). A) dorsal, B) ventral.

Fig. 6. A gynandromorph, or sexual mosaic, which appears to be more than 60% female (from brood #3622, pupal wt. 1.2866, ex. ova, reared in 1986, eclosed on 12 Aug. 1986) from a pure *P. g. glaucus* lineage (in which the mother was the daughter of a dark morph female collected in May 1986 in Hocking Co., Ohio by S. Stribling and the father was the son of a dark morph female collected in July 1985 in Adams Co., Ohio by J. Thorne and MHE). A) dorsal, B) ventral.

Fig. 7. A gynandromorph, or sexual mosaic, which appears to be more than 60% male (from brood #2830, pupal wt. 1.1341, ex. ova, reared in 1985, eclosed on 1 June 1986) from a dark morph *P. g. glaucus* female (reared from eggs obtained from a dark morph female wild collected in Clay Co., W. Virginia on 12 July 1984 by W. Warfield and MHE) mated to a wild collected *P. rutulus* male (reared from eggs obtained from a wild female collected by R. Dowell in Sacramento Co., CA). A) dorsal, B) ventral.

Fig. 8. A gynandromorph, or sexual mosaic, which appears to be more than 75% female but with male claspers (from brood #3935, pupal wt. 1.5321, ex. ova, reared in 1986, eclosed 14 Sept. 1986) from a wild collected dark morph *P. g. glaucus* female (collected in Scioto Co., Ohio on 4 July 1986 by J. Thorne and MHE). A) dorsal, B) ventral.

Fig. 9. A gynandromorph which appears to be more than 80% male (from brood #2025, pupal wt. 1.1541, ex. ova, reared in 1984, eclosed on 12 May 1985) from a yellow morph *P. g. glaucus* female wild collected in Clarke Co., Georgia (collected on 29 Aug. 1984 by J. Maudsley). A) dorsal, B) ventral.

Fig. 10. A gynandromorph which appears to be more than 90% male (from brood #631, pupal wt. 0.9980, ex. ova, reared in 1983, eclosed on 25 Oct. 1984, was paired to 2054 but produced no progeny) from a yellow morph *P. g. glaucus* female wild collected in Adams Co., Ohio (collected on 9 July 1983 by W. Warfield and

MHE). A) dorsal, B) ventral.

Fig. 11. A female color mosaic (ex. ova, reared in 1981 by D. Ritland and J. M. S., eclosed Aug. 1981) from a normal appearing dark morph *P. g. glaucus* female (collected in Dane Co., Wisconsin in June 1981 by P. Kingsley and D. Ritland). A) dorsal, B) ventral.

Fig. 12. A female color mosaic (from brood #1064, pupal wt. 1.2526, ex. ova, reared in 1984, eclosed on 9 July 1984) from a wild dark morph *P. g. glaucus* female (collected in Oglethorpe Co., Georgia on 14 Apr. 1984 by J. Maudsley). A) dorsal, B) ventral.

Fig. 13. A female color mosaic (from brood #1999, pupal wt. 1.2960, ex. ova, reared in 1984, eclosed on 10 May 1985) from a wild dark morph *P. g. glaucus* female (collected in Rock Island Co., Illinois on 25 Aug. 1984 by W. Warfield). A) dorsal, B) ventral.

Fig. 14. A female color mosaic (from brood #658, pupal wt. 0.9439, ex. ova, reared in 1983, eclosed 2 June 1984) from a wild dark morph *P. g. glaucus* female (collected in Adams Co., Ohio on 9 July 1983 by W. Warfield and MHE). A) dorsal, B) ventral.

Fig. 15. A female color mosaic (from brood #1128, pupal wt. 1.5200, ex. ova, reared in 1984, eclosed 12 July 1984) from lab paired parents which were progeny of two wild dark morph *P. g. glaucus* females (both collected in Adams Co., Ohio and 9 July 1983 by W. Warfield and MHE). A) dorsal, B) ventral.

Fig. 16. A female color mosaic (from brood #3973, pupal wt. 1.1323, ex. ova, reared in 1986, eclosed 18 Sept., 1986) from a wild dark morph *P. g. glaucus* female (collected in Adams Co., Ohio on 5 July 1986 by J. Thorne and MHE). A) dorsal, B) ventral.

Fig. 17. A female color mosaic (from brood #3800, pupal wt. 1.4466, ex. ova, reared in 1986, eclosed 7 Oct. 1986) from a wild dark morph *P. g. glaucus* female (collected in Adams Co., Ohio on 6 July 1986 by J. Thorne, and MHE). A) dorsal, B) ventral.

Fig. 18. A wild collected *P. g. glaucus* female color mosaic (assigned #729 and set up for oviposition but died laying only one infertile egg: collected in Dane Co., Wisconsin on 7 Aug. 1983 by MHE). A) dorsal, B) ventral.

Fig. 19. A wild collected *P. g. glaucus* female color mosaic (assigned #736 and set up for oviposition but died laying no eggs: collected in Dane Co., Wisconsin on 7 Aug. 1983 by W. Warfield). A) dorsal, B) ventral.

Fig. 20. Fourteen female siblings with various color mosaic patterns were generated from one brood (#688, ex. ova, reared in 1983) from a normal appearing wild dark morph *P. g. glaucus* female (collected in Dane Co., Wisconsin on 1 Aug. 1983 by W. Warfield). Nine of those female siblings are shown here. A) dorsal, B) ventral.

A)	Pupal wt. 1.2253 g;	eclosed 25 Oct. 1984
B)	" wt. 0.9834 g;	" 29 May "
C)	" wt. 1.1072 g;	" 30 May "
D)	" wt. 1.2296 g;	" 25 Oct. "
E)	" wt. 1.1742 g;	" 25 Oct. "
F)	" wt. 1.3444 g;	" 1 June "
G)	" wt. 1.2375 g;	" 25 Oct. "
H)	" wt. 1.2555 g;	" 25 Oct. "
I)	" wt. 0.9885 g;	" 31 May "

Fig. 21. A wild collected *P. g. glaucus* female color mosaic (assigned #1039 and set up for oviposition: she laid 5 eggs which produced 2 larvae. One reached the adult stage as a normal appearing male which was not mated.) wild collected (in Jasper Co., Texas in April 1984 by JMS and MHE). A) dorsal, B) ventral.

Fig. 22. A wild collected *P. g. australis* female color mosaic (collected in Highlands Co., Florida in Apr. 1981 by B. Giebink, JMS and MHE). A) dorsal, B) ventral.

Fig. 23. A female color mosaic (from brood #1914, pupal wt. 0.9309, ex. ova,





reared in 1984, eclosed 28 Oct. 1984) from a dark morph *P. g. glaucus* female (the daughter of a lab pairing of a dark morph *P. g. glaucus* female reared from stock collected in Oglethorpe Co., Georgia in April 1984 by J. Maudsley, mated to a wild *P. g. glaucus* male collected in Richland Co., Wisconsin on 7 June 1984 by S. Sippl, and JMS) lab mated to a wild *P. g. glaucus* male (collected in Rock Island Co., Illinois on 11 Aug. 1984 by W. Warfield). A) dorsal, B) ventral.

Fig. 24. A female color mosaic (from brood #3604, pupal wt. 1.4616, ex. ova, reared in 1986, eclosed 4 Aug. 1986) from a dark morph *P. g. glaucus* female (the daughter of a wild dark morph *P. g. glaucus* female, #3145 collected in Habersham Co., Georgia in Aug. 1985 by J. Maudsley) lab mated to a *P. g. glaucus* male (the son of a wild dark morph *P. g. glaucus* female, #2868, collected in Adams Co., Ohio on 9 July 1985 by J. Thorne and MHE).

Fig. 25. A female color mosaic (from brood #3770, pupal wt. 1.7029, ex. ova, reared in 1986, eclosed 25 Aug. 1986) from a dark morph *P. g. glaucus* female (the daughter of a wild dark morph *P. g. glaucus* female, #3104, collected in Athens Co., Georgia in Aug. 1985 by  $\Delta$ ) lab mated to a wild *P. g. canadensis* male (collected in Tompkins Co., N.Y. by R. Lederhouse on 17 June 1986). A) dorsal, B) ventral.

Fig. 26. A female color mosaic (from brood #1534, pupal wt. 1.3389, ex. ova, reared in 1984, eclosed 3 Aug. 1985) from a dark morph *P. g. glaucus* female (the daughter of a wild dark morph *P. g. glaucus* female, #1038, collected in Jasper Co., Texas on 9 April 1984 by JMS and MHE) lab mated to a wild *P. g. canadensis* male (collected in Juneau Co., Wisconsin on 18 June 1984 by W. Warfield). A) dorsal, B) ventral.

Fig. 27. A female color mosaic (from brood #1351, pupal wt. 1.2429, ex. ova, reared in 1984, eclosed 14 May 1985) from a dark morph *P. g. glaucus* female (the daughter of a wild dark morph *P. g. glaucus* female, #1025, collected in Newton Co., Texas in April 1984 by JMS and MHE) lab mated to a wild *P. g. canadensis* male (collected in Wood Co., Wisconsin on 12 June 1984 by C. Plazk, Y. Allen, K. Hale, and W. Warfield). A) dorsal, B) ventral.

Fig. 28. A female color mosaic (from brood #1348, pupal wt. 1.1453, ex. ova, reared in 1984, eclosed 1 July 1986) from a dark morph *P. g. glaucus* female (the daughter of a wild dark morph *P. g. glaucus* female with yellow discal cells, #1231, collected in Oglethorpe Co., Georgia in May 1984 by J. Maudsley) lab mated to a wild *P. g. canadensis* male (collected in Green Lake Co., Wisconsin on 12 June 1984 by J. Thorne, S. Sippl, and MHE). A) dorsal, B) ventral.

Fig. 29. A female color mosaic (from brood #717, pupal wt. 1.3006, ex. ova, reared in 1983, eclosed 26 Sept. 1983) from a "peppered"-colored yellow female (from brood #558; a dark morph female GA Pgg x Pgc, backcrossed to a Pgg from Wisc.) mated to a wild *P. g. australis* male (collected in Highlands Co., Florida on 3 Aug. 1983 by JMS). A) dorsal, B) ventral.

Fig. 30. A female color mosaic (from brood #4230, pupal wt. 1.0948, ex. ova, reared in 1986, eclosed 4 Oct. 1986) from a dark morph *P. g. glaucus* female (the daughter of a dark morph *P. g. glaucus* female, #3540, wild collected in Champaign Co., Illinois in June 1986 by M. Berenbaum) lab mated to a wild *P. alexiars* male (collected in Nuevo Leon, Mexico 2-3 Aug. 1986 by W. Warfield, D. Robacker, and MHE). A) dorsal, B) ventral.

and 19). Fourteen other *P. g. glaucus* mosaics are all siblings from one wild collected female from Dane Co., Wisconsin (e.g., Fig. 20). Two field captured females from Texas were mosaics (Table 6; Fig. 21).

Of the six lab-reared mosaics that were not of "pure" subspecies lineage four are progeny of subspecies crosses between *P. g. glaucus* females and *P. g. canadensis* males (Table 6). Three of these are yellow females with the exceptional and asymmetrical color being black (Figs. 26-28) while the fourth is an intermediately colored female with the exceptional color being yellow (Fig. 25). The fifth non-pure *P. g. glaucus* mosaic is the product of a lab pairing involving all three *P. glaucus* subspecies as ancestors. The mosaic is 50% *P. g. australis*, 12.5% *P. g. canadensis*, and 37.5% *P. g. glaucus* (Fig. 29). A sixth mosaic arose from a *P. g. glaucus* paired with a male *P. alexiars garcia* (Fig. 30).

## Discussion

The reported frequency of color mosaics or gynandromorphs is quite low. We have reared more than 28,000 individuals of the *Papilio glaucus* complex (1981-1986) and have observed only 37 color mosaics and only 5 perfect or nearly perfect bilateral gynandromorphs. While from previous literature records it would seem that the "blend zone" (i.e. the zone of potential/probable hybridization) across the Great Lakes and Appalachian Mountain region has accounted for most previously reported aberrant types of *P. glaucus* (Edwards, 1868, 1884; Skinner and Aaron, 1888; Ehrman, 1893; Howard, 1899; Clark and Clark, 1951; Ehle, 1981; Scriber et al, 1985; H. Romack, pers. comm.), we have in this 5-year period observed mosaics in stock from Georgia, Texas, Illinois and Ohio as well as Wisconsin. In addition to our Dane County field-captured mosaics (near the zone of suspected hybridization), color mosaics exist from Richmond County, NY (5 July 1971; A.M. Shapiro; currently in the University of California-Davis Collection) and Washington County, PA (9 May 1927; George F. Patterson Collection at Pennsylvania State University), both also near the proposed blend zone (see Ritland and Scriber, 1985; Scriber and Hainze, 1987).

Since in our studies, 4 of 5 perfect or nearly perfect bilateral gynandromorphs are progeny of subspecies or species crosses in the *P. glaucus* species complex, and since 32 of 37 mosaics are progeny of "pure" (i.e. single subspecies) lines, it could be argued that factors inducing the expression of gynandromorphic traits are likely to be different than factors inducing the expression of mosaic traits. In fact, for the occurrence of mosaics the observed distribution between inter-taxa versus intra-taxa crosses does not differ from the expected ( $n = 5105$ , Chi square,  $p = 0.25$ ), whereas for the near perfect bilateral gynandromorphs significantly more resulted from the inter-taxa crosses ( $n = 11, 112$ , Fisher Exact test,  $p < 0.038$ ).

The mechanism(s) by which hybridization may catalyze these events leading to color/sexual abnormalities is uncertain at this time. Clarke

and Clarke (1983; see also Scott, 1986) suggest that in *P. glaucus* maleness is dependent upon the presence of two X chromosomes and femaleness is dependent upon a single X chromosome (the Y chromosome assumed to be relatively inert, except of course that it carries the locus for dark morph color; Clarke and Sheppard, 1962; Clarke et al., 1976). If this is true (cf. Tazima, 1964; where femaleness in silk moths may be related to the Y chromosome), then the *P. glaucus* sexual mosaics in the Strecker collection may represent the results of either non-disjunction or double fertilization (Clarke and Clarke, 1983). Three specimens are figured by Clarke and Clarke: 1) The female half black/half yellow may be the result of non-disjunction, i.e. XY/XO with the gene for melanism on the Y and the XO half being yellow; 2) the gynandromorph which is approximately half black (female) and half yellow (male) may be the result of a double fertilization (i.e. XX/XY); and 3) a sexual mosaic specimen (a partial mosaic described by Howard, 1899) could be the result of XX/XY (non-disjunction) or XY/XO (double fertilization). While Clarke and Clarke were not aware of the potential hybridization of *P. g. glaucus* with *P. g. canadensis*, we now suggest with our laboratory results that hybrid individuals in the "blend zone" may indeed be naturally predisposed to non-disjunction or chromosome loss as appears to be the case with other *Papilio* hybrids (see Clarke et al., 1977). In fact, we also have evidence suggesting the loss of a segment of the Y-chromosome controlling the melanic (dark) background coloration in brood number 674 reared in 1983 (with transfer of this chromosome fragment independently, via a crossover or via a non-disjunction) with the melanic locus to at least one of the male sibs!). This aberrant male, when mated to a virgin *P. g. canadensis* from northern Wisconsin and to a yellow morph *P. g. glaucus* female from a yellow morph lineage from Ohio, produced daughter progeny which were both typical dark morph and typical yellow morph (Scriber et al., 1987). Never before has any male *P. glaucus* been known to transmit the trait for female melanism (see Scriber and Evans, 1986).

The ability to distinguish between color mosaics and sexual mosaics is not easy, even with the distinctive pattern of the melanic form female. It is even more difficult to distinguish between yellow morph gynandromorphs (where the male and female regions differ from each other both phenotypically and in genetic constitution) and intersexes (where male and female regions appear phenotypically different, but have identical chromosomal constitution: see Whiting et al., 1934; Douth and Smith, 1950; Clarke and Ford, 1980). We hope that additional studies will clarify the genetic basis of gynandromorph production (see reviews by Cockayne, 1935; Drescher and Rothenbuhler, 1963), and of the differential suppression (modification) of female phenotypes dark/yellow polymorphism in *Papilio glaucus* due to hybridization. Some morphological characteristics differ between the male and female halves of the F<sub>1</sub> specimens figured (Fig. 1 and Fig. 2) as well as the obvious differences in melanism in Fig. 3. The usefulness of developmental physiology

studies in this regard would be significant, especially since the color patterns on the upper and lower surfaces of Lepidoptera wings develop independently (see Nijhout, 1981 for a discussion), and can be modified by environmental temperature (Ritland, 1983).

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